

TOO WET FOR AQUATIC PLANTS?
FLORISTIC COMPOSITION AND PHYTODIVERSITY IN THE
WETLANDS ALONG THE BASE OF THE BOLIVIAN ANDES

NUR P. RITTER

California State University, Stanislaus,
Endangered Species Recovery Program,
1900 N. Gateway Ave., Fresno, CA 93727
e-mail: nur@botanize.com

ABSTRACT. An investigation of the vascular plant flora of the wetlands in the Chapare, an extremely high-precipitation region along the base of the Bolivian Andes, was undertaken from 1994 to 1996. One hundred fifty-one species in 52 families and 107 genera were identified as occurring in the region's wetlands. In contrast to the terrestrial flora of the Chapare and of other regions in the Andean forelands, Chapare wetlands were found to be characteristically species-poor (5–49 species). Nevertheless, the Chapare wetland flora contained a number of rare or noteworthy species, and represented the southern distributional limit for a number of taxa. The diversity of Chapare "wetland species" (i.e., species considered to be strongly associated with Neotropical wetlands) was low relative to other South American lowland regions when considered in terms of total number of species and from species-area curves. A regional trend toward fewer wetland species with increased precipitation was apparent; however, data supporting this relationship were inconclusive. Despite low floristic similarities (Sørensen's Index) between study sites, the majority of the Chapare study sites were closely situated in an ordination by Detrended Correspondence Analysis (DCA) of the floras of 46 wetlands distributed throughout Bolivia. At the regional scale, floristic similarities with other regions considered in this study were relatively low. As might be expected, an ordination of the regional data indicated that the Chapare wetland flora was most strongly associated with the other lowland Bolivian regions, while the most geographically distant regions were also the furthest removed in ordination space.

Key Words: Neotropics, Bolivia, Chapare, wetlands, aquatic plants, phytodiversity

The region along the base of the Cordillera Oriental (Eastern Range) of the Bolivian Andes in the Department of Cochabamba is colloquially referred to as the *Chapare*. At times, the Andean slopes are also included in the delineation of the Chapare (e.g., Guyot and Watson 1994; Solomon 1989), but the name is most often used solely in reference to the lowlands, a usage that is also applied here. The Chapare (Figure 1) occupies the transition between the Andes and the extensive floodplain that extends northwards through the Department of Beni and eastwards to the Brazilian Shield. The largest part of this floodplain, the Beni basin, is characteristically quite level and occupies elevations between 150–250 m

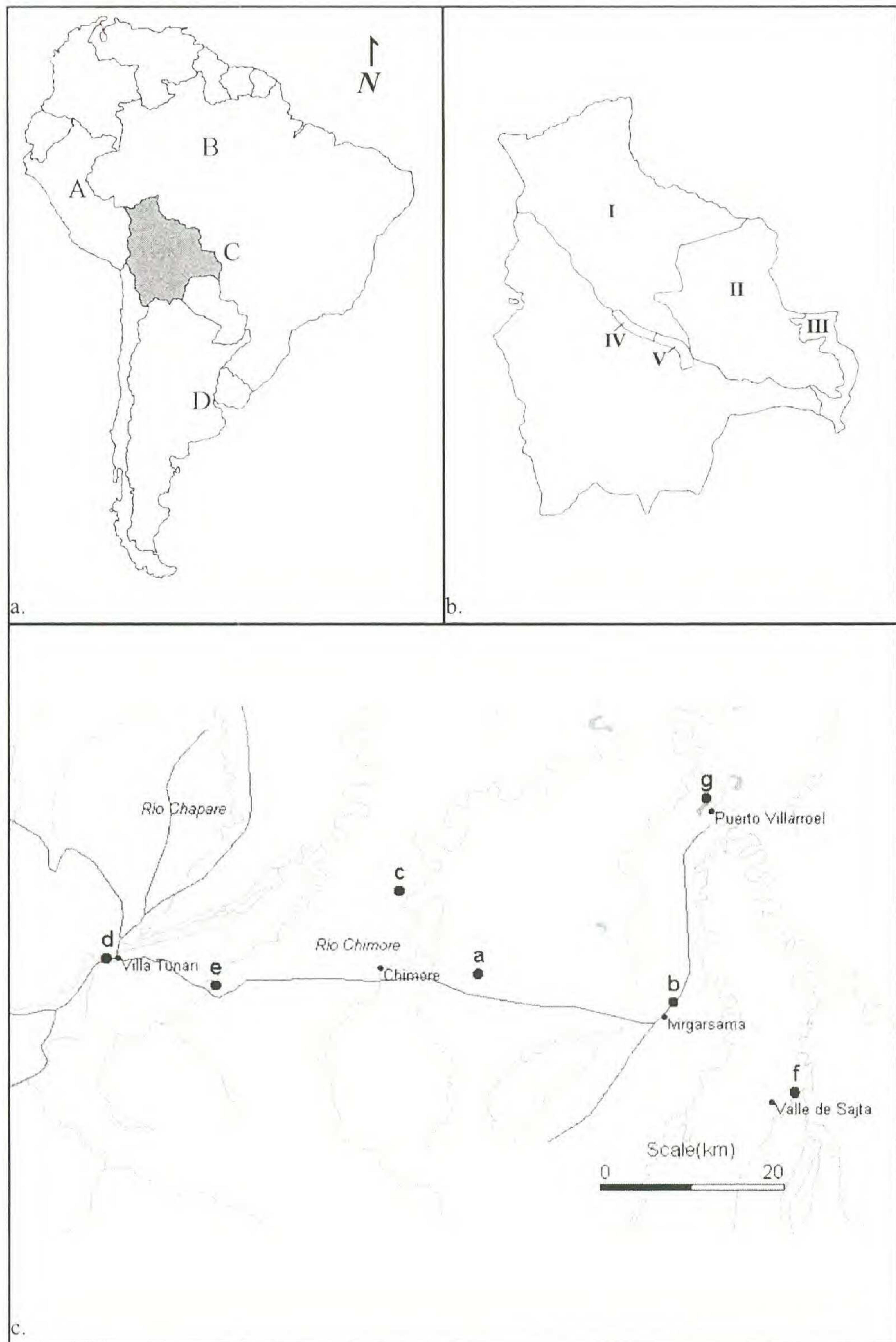


Figure 1. Study site locations. a. South America, with approximate centers of extra-Bolivian Operational Geographic Units (OGUs): A. Lowland Amazonian Peru; B. Central Amazonia; C. Brazilian portion of the Gran Pantanal de Mato Grosso; D. Río Paraná Delta. Bolivia occupies the shaded portion in the center of the continent. b. Bolivia, with approximate delineation of the Bolivian OGUs: I. White-water

(Killeen et al. 1993; Plafker 1964). Topography in the Chapare is more variable, with low hills creating a dissected relief. Although the Chapare region includes territory from three provinces (Chapare, Tiraque, and Carrasco) the colloquial name for the region is quite functional, circumscribing an area characterized by high rainfall, high temperatures, low elevations, and (previously) extensive tracts of rainforest. Although the precise geographic limits are not clearly defined, the Chapare has an area of approximately 3000 (Henkel 1995) to 4000 km² (determined from maps using the “cut and weigh method,” cf. Lind 1985).

The Chapare is situated in an “inside corner” of the Andes, formed by a change from an approximately southwest to northeast orientation of the mountains to a more eastern bearing. This region and the adjacent Andean slopes receive the highest amount of rainfall in Bolivia. Maximum mean annual precipitation in the Chapare reaches an estimated 4900 mm/yr, with a maximum hydrologic year of 6900 mm (Morris et al. 1983). Rainfall is even greater in the lower Andean slopes just above the Chapare, where mean annual precipitation is estimated to reach 6000 (Moraes and Beck 1992) to 7000 mm/yr (Guyot and Watson 1994). Rainfall decreases northwards away from the mountains and eastwards toward the City of Santa Cruz (Morris et al. 1983). Thus, in the approximately 70 km between the two most disjunct Chapare study sites (see Materials and Methods) mean annual precipitation ranged from about 2500 mm to > 4500 mm (estimated from isohyets presented in Morris et al. 1983). Despite abundant precipitation, the region still experiences a few months of low rainfall (roughly, June to August), such that many of the area’s small ponds and roadside ditches dry out completely. Mean monthly temperatures range from 20° to 38°C (Henkel 1995), with a mean annual temperature of 21.8° (Maldonado et al. 1996) to 25°C (Killeen et al. 1993). Temperatures in the region always remain above 0°C.

The slopes of the Cordillera Oriental are precipitous, with the transition between montane peaks (> 4500 m) and the lowlands occurring over a short distance (ca. 30–40 km, *linea recta*). The slopes above the Chapare are characterized by deposits of sedimentary rocks that consist primarily of shales and may be greater than 200 m in thickness (Morris et al. 1983).

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Floodplain; II. Chiquitanía; III. Bolivian portion of the Gran Pantanal de Mato Grosso; IV. Chapare; V. Andean Piedmont. c. Location of the Chapare (Bolivia) study sites: a. Mariposa Wetland; b. Ivirgarsama Marsh; c. Senda F Wetland; d. Villa Tunari Pond; e. Sinahota Pond; f. Valle de Sajta Curichi; g. Puerto Villarroel Laguna.

These substrata and their derived soils are unstable and tend to erode rapidly when stripped of vegetation (Morris et al. 1983); rates of erosion are extremely variable, ranging from an estimated 1000–20,000 t/km²/yr (Guyot and Watson 1994). At the base of the mountains, the shales are overlain by deposited alluvial materials. These deposits are generally arrayed sequentially from coarse materials at the foothills to finer-grained sediments away from the mountains (Morris et al. 1983).

The rivers draining the steep Andean slopes arrive at the Chapare with great force and are extremely dynamic upon reaching the easily erodible soils. Erosion and sedimentation occur rapidly (Morris et al. 1983), with lateral channel migrations a constant feature of the Chapare's rivers. Salo et al. (1986) analyzed channel dynamics in Peruvian Amazonia by comparing aerial photographs from 1962–63 with a 1976 Landsat (satellite) image. They estimated that for their area of study in lowland Peru the mean lateral erosion rate of meander bends during this period was 12 m/yr (Salo et al. 1986). It seems reasonable that channel migration in the Chapare rivers could be of a similar magnitude.

The rivers of the Beni basin are characteristically very turbid (Guyot and Watson 1994), corresponding to white-water rivers (*sensu* Sioli 1975). On the floodplain, the rivers are an opaque brown from their large load of suspended fine particles; however, river water in the Chapare is generally much more transparent. This phenomenon presumably occurs because the rivers and streams that drain the Andean slopes are generally clear and only carry large amounts of sediments when the vegetative cover, which protects the weathered substratum, is subjected to landslides and other large-scale disturbances (cf. Sioli 1984).

Historically, the Chapare's terrestrial vegetation was dominated by tall forest, characterized by high diversity (Killeen et al. 1993). However, during the 1960s and '70s the government advanced colonization of the region, constructing roads to and within the Chapare and apportioning 202,000 ha of land for new colonists (Henkel 1995). Logging has been extensive and large portions of the region have been cleared for agriculture, with approximately 80% of the land dedicated to the cultivation of coca (*Erythroxylum coca*) and the remaining 20% to other crops. Consequently, the greatest part of the Chapare's remaining forested habitats are secondary forest.

There have been few limnological investigations of the Chapare's aquatic habitats, and references to the aquatic flora are nearly nonexistent. Limnological studies were undertaken by Barra et al. (1990), Cadima (1990), and Maldonado et al. (1996). Of these, the sole reference to the vascular flora was from Maldonado et al., who listed the macrophytes

Table 1. Study sites of the Chapare region (Bolivia), with elevation, approximate area, number of species encountered, approximate location, and dates visited.

Study Site Name	Elev. (m)	Area (ha)	Spp.	Location	Dates Visited
Mariposa Wetland	220	1.5	49	17°01'S, 65°02'W	11/27/94; 3/5/95; 6/8/95; 11/1/96
Ivirgarsama Marsh	200	0.7	44	17°01'S, 64°50'W	2/23–24/96; 5/10/96; 10/27/96
Senda F Wetland	200	0.2	19	16°52'S, 65°08'W	6/1/94; 11/11/94; 3/4/95
Villa Tunari Pond	300	0.3	11	17°01'S, 65°26'W	11/12/94; 3/5/95; 6/8/95
Sinahota Pond	240	0.15	9	17°00'S, 65°18'W	11/12/94; 6/8/95
Valle de Sajta	220	0.2	6	17°07'S, 64°43'W	3/20/95
Curichi					
Puerto Villarroel Laguna	200	30.0	5	16°49'S, 64°48'W	3/19/95; 11/1/96

encountered in a series of lakes on the Río Ichilo floodplain. Additional information comes from Jiménez (1984), who listed various wetland species in his account of the flora of the Department of Cochabamba.

In the present study, I undertook a botanical survey of the wetlands of the Chapare as a portion of a larger study of the wetlands of Bolivia (Ritter 2000). My specific objectives were as follows: 1) to prepare a provisional checklist of the vascular plant species associated with Chapare wetland habitats; 2) to identify rare or noteworthy species from these habitats; 3) to estimate the range of site-level vascular plant species richness; 4) to compare species richness in the Chapare wetland flora to lowland regions in Bolivia and other South American countries; and 5) to examine floristic similarities among the Chapare wetland flora and these regions. To these ends, the flora of the Chapare wetlands is listed and noteworthy species are discussed. Comparisons of species richness and floristic similarity are made between study sites. At the regional level, comparisons are made among the Chapare wetland flora and seven lowland regions in Amazonia and extra-Amazonian South America.

MATERIALS AND METHODS

Study sites. Within the Chapare, seven wetland systems were established as study sites (Table 1; Figure 1). Although field research was concentrated on these systems, additional botanical collecting was undertaken in a variety of wetland types (e.g., small marshes, streams,

rivers, oxbow lakes, strand lakes, and inundated roadside ditches). Brief descriptions of the study sites follow.

1. Mariposa Wetland.

The Mariposa Wetland was located alongside the highway from the Chapare to Santa Cruz, approximately 1.5 km east of the community of Mariposa. The system consisted of two small (< 0.3 ha) ponds fringed with a strip of marshy habitat. The ponds occupied shallow depressions (ca. 2 m deep) that were created when fill for an adjacent highway was excavated from the site. The marsh was situated between the ponds and the highway and was essentially a wide (ca. 50 m) section of the "borrow canals" that typically flanked the highway and other roads in the region. Although these canals extend for many kilometers, investigations of the Mariposa "system" were limited to an approximately 200 m long section of marsh, centered on the two ponds. A small, seasonal stream delineated the western edge of the study site. Total study site area was approximately 0.8 ha.

In contrast to many similar small bodies of water in the Chapare, the ponds contained water throughout the year, suggesting that they received some subsurface water inflow. During the dry season, standing water disappeared from most areas of the marsh; soil conditions varied from fairly dry to saturated during this period. Although this system undoubtedly received substantial inputs of runoff from adjacent uplands during the rainy season, there were no large rivers near the site. Thus, the system did not appear to receive the periodic influxes of water-borne sediment that were characteristic of many of the Chapare's aquatic habitats.

2. Ivirgarsama Marsh.

The Ivirgarsama Marsh was located alongside the unpaved road that connected the highway to Santa Cruz with the town of Puerto Villarroel. The system was composed of a small (ca. 0.2 ha) shallow pond with an adjoining (ca. 0.5 ha) marshy area in the area between the pond and the road. Smaller sections of marsh also occurred along the other edges of the pond. A narrow stream flowed through the system, entering the pond at one end and discharging through the marsh at the far end of the system. As with the Mariposa Wetland, the marsh was essentially a widening of a typical roadside borrow canal, however the pond at the Ivirgarsama Marsh appeared to be of natural origin. The Ivirgarsama Marsh was unique among the Chapare study sites because of the well-developed floating mats of vegetation present along the edges of the pond.

3. Senda F Wetland.

The Senda F Wetland was located between the town of Chimoré and the Río Chapare. The system was situated adjacent to an unpaved road and was contiguous with the borrow canals that flanked the road. A small stream flowed into the southeast corner of the marsh, and a number of small, fairly deep pools were present. Hence, habitat heterogeneity was much higher than was typical for the region's roadside canals. The area surveyed was approximately 80 m long with a maximum width of about 15 m on either side of the road. Water levels at the site fluctuated seasonally and standing water was absent from parts of the marsh during the driest portions of the year.

4. Villa Tunari Pond.

The Villa Tunari Pond was a small pond located alongside the Cochabamba-Santa Cruz highway, approximately 4 km east of the town of Villa Tunari. As it was situated near to the start of the ascent of the Cordillera Oriental (Eastern Range) of the Andes, the system occupied a slightly higher elevation (300 m) than the other Chapare sites. During the dry season, the pond's surface covered an area of about 0.3 ha; during the rainy season, large portions of the upland areas adjacent to the pond became shallowly inundated and the limits of the "system" were indistinct. Maximum depth during the rainy season was on the order of 2.0–2.5 m; water levels dropped significantly during the dry season. Although the basin was never observed to be entirely without standing water, it seems likely that this might occur during dry years.

5. Sinahota Pond.

The Sinahota Pond was another small (approximately 0.15 ha) seasonal pond situated alongside the Cochabamba-Santa Cruz highway, approximately 2 km west of the town of Sinahota. Maximum depth during the rainy season was about 2.0 m; during the dry season the system dried out completely. The basin was fairly steep-sided and, in contrast to the Villa Tunari Pond, inundation did not appear to extend to the surrounding areas during typical high water stages.

6. Valle de Sajta Curichi.

In the Bolivian lowlands, a "curichi" is a system that occupies a section of a former river channel, and which normally does not dry-down completely during the dry season (Beck 1984). The Valle de Sajta Curichi consisted of two small ponds separated by a narrow (10 m) strip of land. The ponds originally comprised a section of a river channel—most likely

the nearby Río Zabala—and developed into their present form after being stranded due to channel migration. The ponds appeared to be connected by a subterranean passage and the system was said to contain water year-round.

7. Puerto Villarroel Laguna.

The Puerto Villarroel Laguna, a large curichi, was the largest and deepest of the Chapare study sites. Despite being located in a region characterized by “white-water,” the system’s water was stained dark from organic acids. Maximum depth was difficult to determine, but appeared to be at least 4 m. The lake’s area as estimated using the cut and weigh method (Lind 1985) on a 1:100,000 scale topographical map, was found to occupy 70 ha; however, during visits to the site the area was visually estimated at about 15 ha. As a compromise, 30 ha. was selected as a rough approximation of the system’s size.

Vegetation sampling. Sampling focused on compiling comprehensive site floras. As noted, the study sites were fairly limited in size (Table 1); it was possible to survey each site in its entirety. Fieldwork was conducted intermittently from June 1994 to November 1996. Sites received multiple visits (Table 1) whenever possible in order to view the systems under different hydrologic conditions and thus to maximize the number of species encountered. Preferably, fieldwork was scheduled so that sites were visited during both the wet and dry seasons, but due to various constraints this was not always possible.

Voucher specimens were made of all species observed at each site and, with one exception, were deposited in the Herbario Forestal (BOLV; Cochabamba) and the University of New Hampshire’s Hodgdon Herbarium (NHA). When available, duplicates were deposited at the Herbario Nacional de Bolivia (LPB; La Paz), the herbarium of the Museo de Historia Natural “Noel Kempff Mercado” (USZ; Santa Cruz), and the Missouri Botanical Garden herbarium (MO). A checklist, including life-form and species abundances at each site, is presented as an Appendix.

Floristic comparisons. A regional checklist of wetland species was compiled from the study sites and augmented by data from general collecting in the Chapare, from the literature, and from exsiccatae listed in the Missouri Botanical Garden database, TROPICOS. Published sources used to augment the checklist were Maldonado et al. (1996), which was incorporated in its entirety, and Jiménez (1984), which was reviewed for species collected from the Chapare.

Table 2. Operational Geographic Units (OGUs) utilized in this study, with estimated total area, number of wetland species, and floristic similarity (Sørensen's Index) between the OGU and the Chapare. Detailed descriptions of the OGUs and an account of the sources used in compiling the floras are given in Ritter (2000).

OGU	Approximate Area (km ²)	No. of Species	Floristic Similarity
Chapare	4000	113	—
Andean Piedmont	5000	244	33.6
White-water Floodplain	325,000	464	31.5
Chiquitanía	190,000	541	28.4
Gran Pantanal (Bolivia and Brazil)	140,000	451	23.4
Central Amazonia (Brazil)	70,700	429	32.8
Lowland Amazonian Peru	533,100	255	28.8
Río Paraná Delta (Argentina)	23,700	297	10.7

Floristic relationships were analyzed at two scales: 1) among study sites and, 2) among regions (mesoregional scale *sensu* McLaughlin 1994). Regional comparisons were made among the flora of the Chapare and the following OGUs (Operational Geographical Unit, cf. Crovello 1981): Central Amazonia (Brazil), Lowland Amazonian Peru, the Río Paraná Delta region (Argentina), the Gran Pantanal de Mato Grosso (Bolivia and Brazil), and three additional areas of lowland Bolivia (the White-water Floodplain, Chiquitanía, and Andean Piedmont regions). For each OGU, estimated total area, total wetland species, and calculated floristic similarities are presented in Table 2. It should be noted that the total number of wetland species included for the Chapare in regional comparisons is less than the number of species listed in the Appendix, as species lacking complete identifications and species not considered to be strongly associated with wetlands were excluded from regional floristic comparisons. Salient characteristics of the OGUs are presented where warranted; detailed descriptions, and an account of the sources used to compile OGU floras are given in Ritter (2000).

Ascription of "wetland species." In order to undertake regional-scale comparisons, a checklist of wetland species (Ritter, unpubl. database) was used to determine species presence in each OGU. A complete account of the sources used in compiling the checklist and a discussion of the criteria used in the ascription of species is presented in Ritter (2000).

Data analysis. Degrees of floristic similarity among OGUs were analyzed using Sørensen's Index (Magurran 1988):

$$S = 2j \div (a + b)$$

where a is the total number of species in OGU 1, b the total number of species in OGU 2, and j the number of species present in both OGU 1 and OGU 2.

As with most similarity indices, Sørensen's Index gives equal weight to all species in calculating floristic similarity. However, shared rare or uncommon species in a pair of OGUs can also serve as valid indicators of floristic similarity (Simberloff and Connor 1979). In order to assess the relative contribution of these species to overall floristic similarity, the frequencies of "species classes" (e.g., species present in all OGUs, species restricted to 2 OGUs, etc.) were graphed. This analysis was not conducted among all OGUs; rather it was restricted solely to comparisons between the Chapare flora and the other OGUs. Because floristic similarities (Sørensen's Index) between the Río Paraná Delta region and all other OGUs were uniformly low, this OGU was excluded from this analysis.

In order to express floristic relationships among all OGUs simultaneously, data were organized into a binary matrix of OGUs versus species (recorded as presence-absence values) and were ordinated using Detrended Correspondence Analysis (DCA; Hill and Gauch 1980). Ordinations were conducted using the software package, PC-ORD (MjM Software, Gleneden Beach, OR).

RESULTS

Vegetation description. One hundred fifty-one species, in 52 families and 107 genera, were identified as being associated with Chapare wetlands (Appendix). The Poaceae (14 genera, 25 spp.) and Cyperaceae (8 genera, 17 spp.) were the best-represented families; *Panicum* (Poaceae, 9 spp.) and *Ludwigia* (Onagraceae, 7 spp.) were the best-represented genera.

Biodiversity. The number of species encountered at the individual sites varied widely (5–49 spp.; Table 1), and was not consistently correlated with area. For example, the largest site (the Puerto Villarroel Laguna, 30 ha) possessed the fewest species (5), and the second largest site (the Mariposa Wetland, 1.5 ha) the greatest number of species (49). In order to compare richness in the Chapare sites with wetlands from other

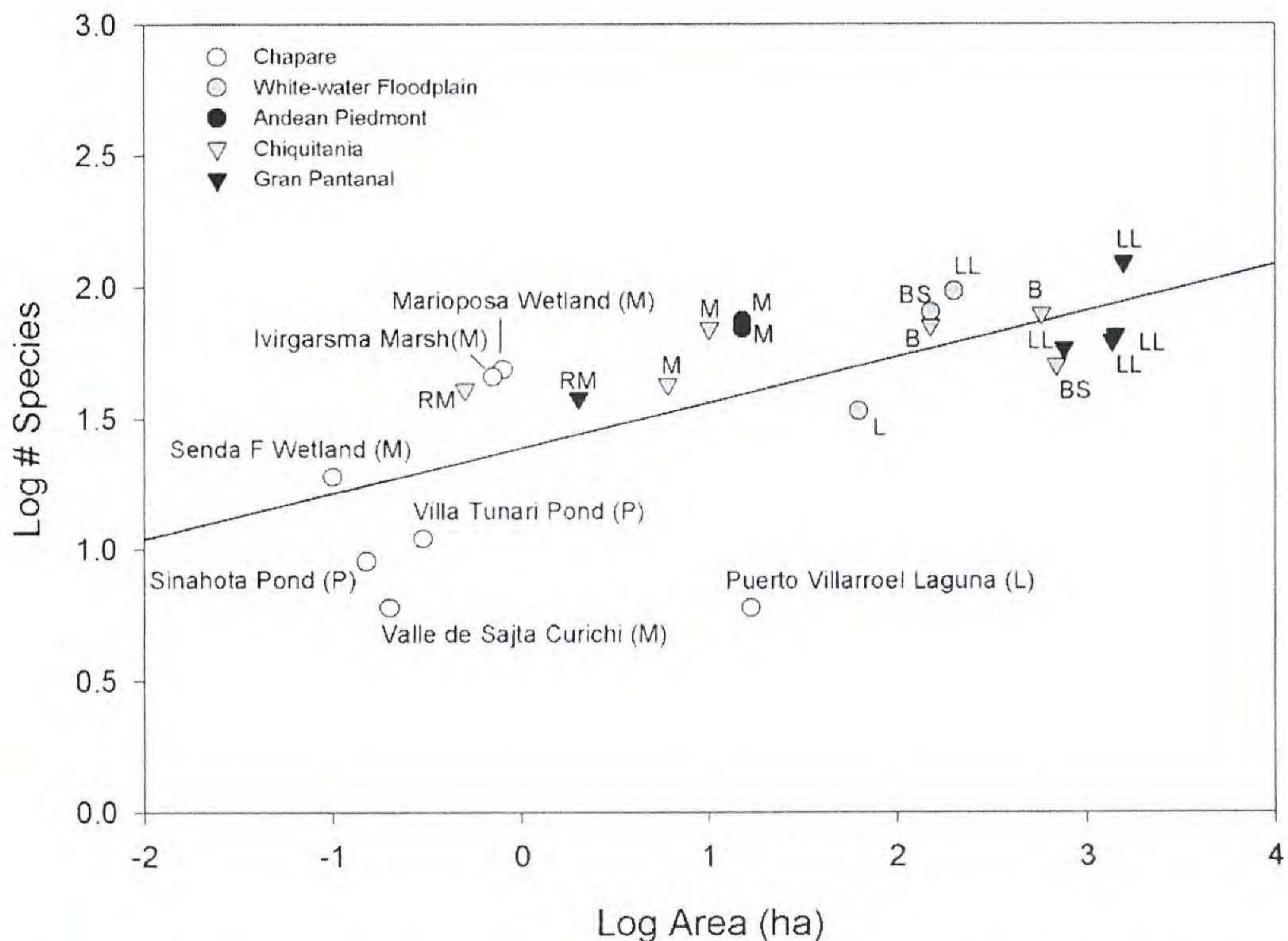


Figure 2. Species-area curve plotted from data from 23 lowland Bolivian wetlands (Ritter 2000), with the Chapare (Bolivia) study sites identified by name. Wetland types: B, bahía; BS, basin swamp; L, small lake (< 500 ha); LL, large lake (> 500 ha); M, marsh; P, pond; RM, riparian marsh. Linear regression: $\log S = 1.39 + 0.17 \log A$; $r^2 = 0.44$.

Bolivian lowland regions, a species-area curve (Figure 2) was plotted from the Chapare data augmented with data from an additional 16 Bolivian lowland wetland systems (Ritter 2000). Study sites situated above the regression line were considered to be relatively species-rich, whereas those below the line were considered to be relatively species-poor. The Chapare sites could generally be characterized as species-poor, as four of the seven systems were located well below the regression line. Of the remaining systems, one was located just above the regression line, and two were situated well above the line.

At the regional level, wetland floras ranged from 113–541 species, with the Chapare possessing the poorest and the Chiquitania the richest floras (Table 2). In order to establish a point of reference for comparing diversity among OGUs, a species-area curve (Figure 3) was plotted using cumulative species (wetland species) and area (total regional area) for the countries of the Neotropics and Mexico (Ritter 2000). This curve was considered to represent the general trend for wetland species richness throughout the Neotropics. Discrete species-area data from the Chapare

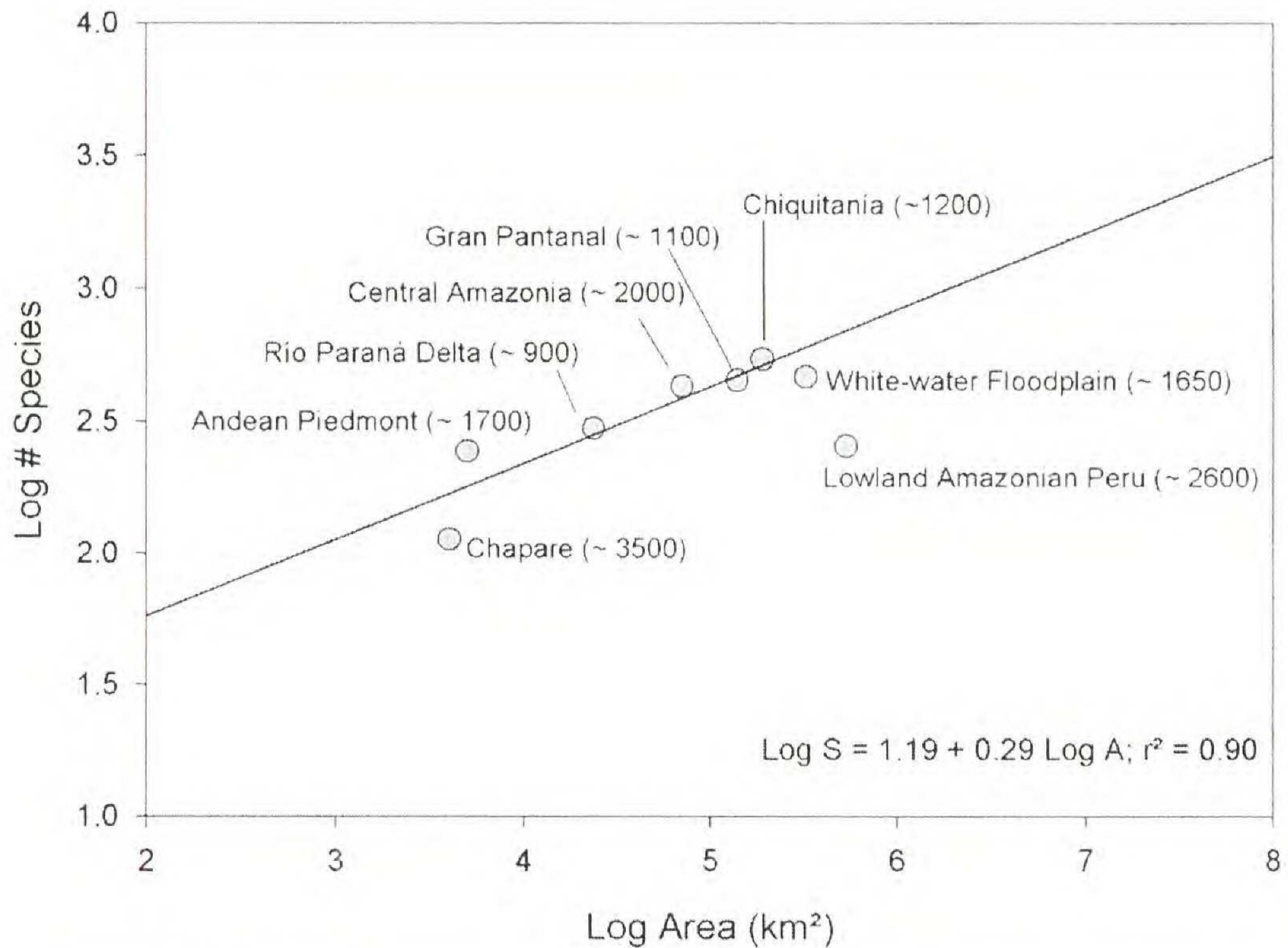


Figure 3. Species diversity of the Operational Geographic Units considered in comparisons with the Chapare (Bolivia) wetland flora. Diversity is relative to a regression line fitted to a species-area curve plotted from cumulative species-area data from the Neotropical countries, including all of Mexico (see Ritter 2000). Values in parentheses indicate estimated mean annual precipitation (mm/yr). Linear regression: $\log S = 1.19 + 0.29 \log A$; $r^2 = 0.90$.

and the other OGUs considered here were added to the plot. It was evident that the Chapare could, indeed, be considered species-poor, as it was situated well below the regression line. Other species-poor OGUs were Lowland Amazonian Peru and the White-water Floodplain. By contrast, the Andean Piedmont region, which is contiguous with the Chapare, constituted the richest OGU.

Floristic similarities. Floristic similarities (Sørensen's Index) between study sites were quite variable, ranging from 0–43.0%. In general, floristic similarities were low, with all but three pairs of sites having similarities below 20%. Despite the generally low floristic similarities, five of the seven Chapare study sites were closely situated in ordination space in an ordination (DCA) of the 46 Bolivian study sites (Figure 4).

At the regional level, the Chapare showed the least floristic similarity (Sørensen's Index) to the Río Paraná Delta region (10.7%; Table 2);

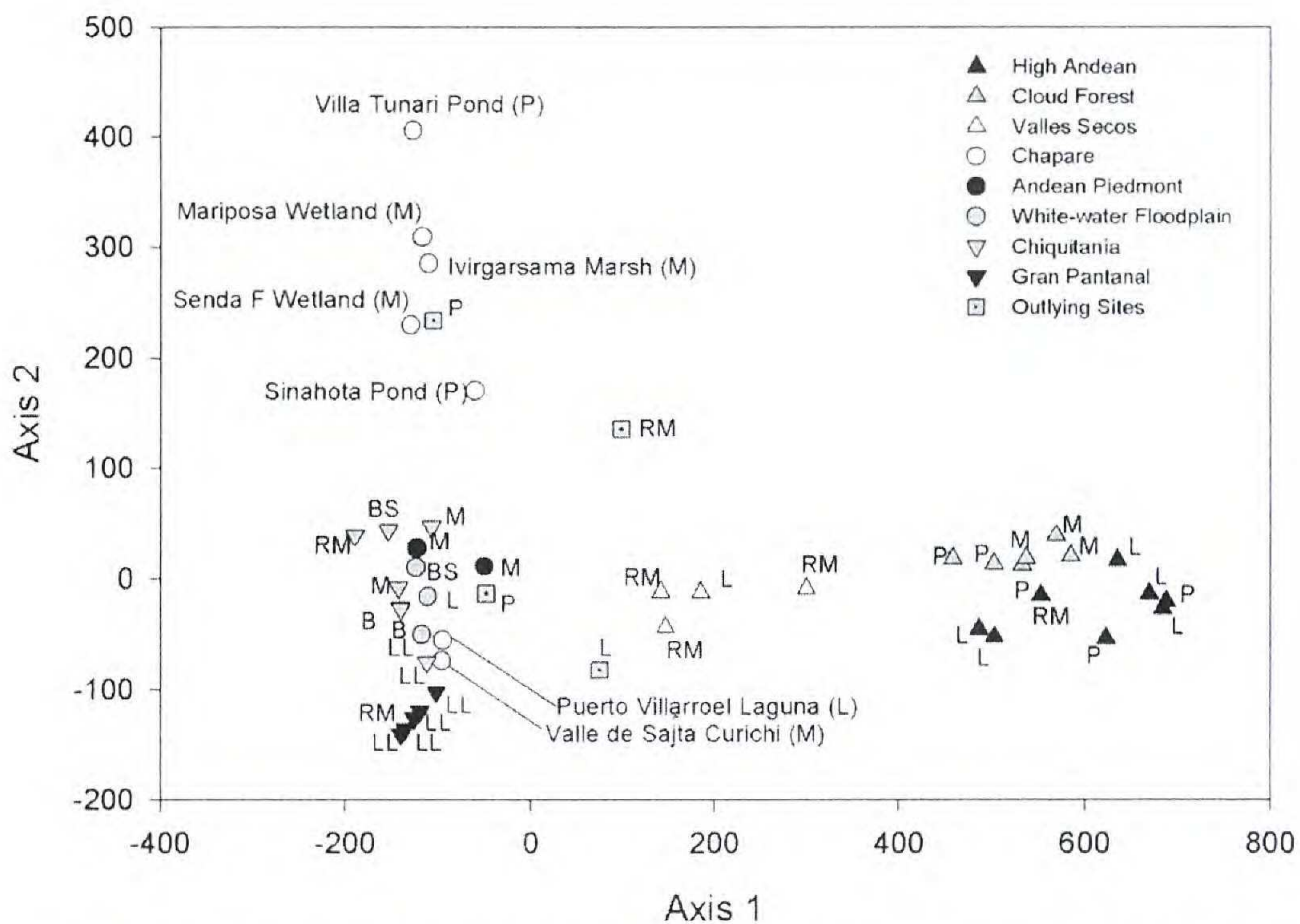


Figure 4. Ordination by Detrended Correspondence Analysis (DCA) of 46 Bolivian study sites. The seven Chapare study sites are identified by name. Key to wetland types: B, bahía; BS, basin swamp; L, small lake (< 500 ha); LL, large lake (> 500 ha); M, marsh; P, pond; RM, riparian marsh. Data from Ritter (2000a).

however, the latter showed few floristic affinities to any of the OGUs (10.7–27.8%). Floristic similarities between the Chapare and the remaining OGUs showed little variability, ranging from 23.4–33.6%. The Chapare was most similar to the Andean Piedmont (33.6%), but this was scarcely higher than the similarities between the Chapare and Lowland Amazonian Peru (32.8%) and White-water Floodplain (31.5%) regions.

An ordination of the regions by DCA (Figure 5) suggested that the floristic relationships were more complex than suggested by Sørensen's Index. The Chapare and the remaining lowland Bolivian OGUs were grouped in fairly close proximity in ordination space. The extra-Bolivian Amazonian OGUs (Lowland Amazonian Peru and Central Amazonia) occupied positions that were disjunct from this grouping. The Río Paraná Delta region formed the endpoint of the first axis, occupying a position far removed from all other OGUs.

A graphical representation of the distribution of species frequency "classes" (Figure 6), demonstrated that the relative contribution of the different classes to floristic similarities was quite variable. In order to facilitate discussion of these relationships, descriptive names were

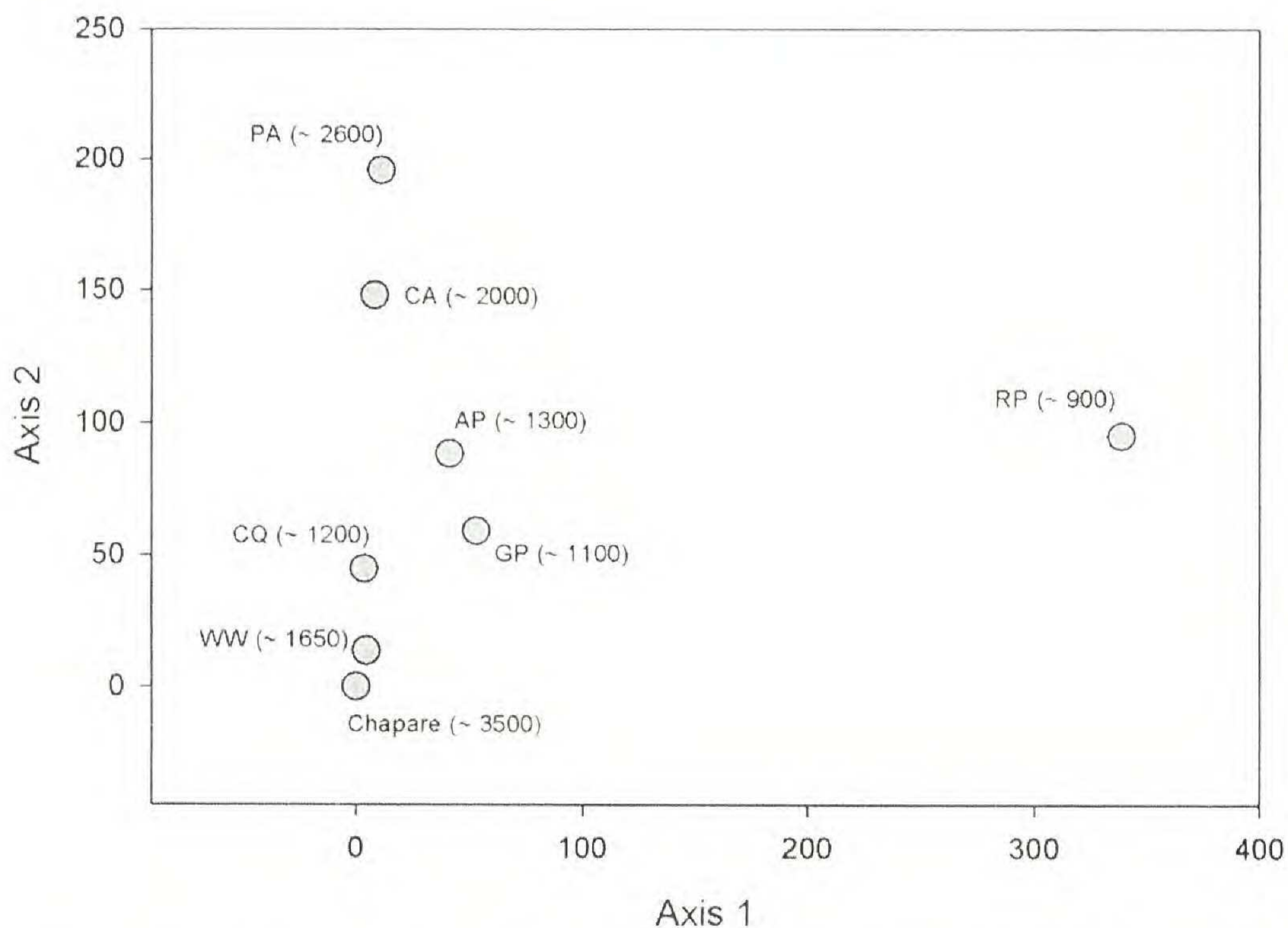


Figure 5. Ordination of the Operational Geographic Units (OGUs) by Detrended Correspondence Analysis (DCA). OGUs: AP, Andean Piedmont; CA, Central Amazonia; CQ, Chiquitanía; GP, Gran Pantanal; PA, Lowland Amazonian Peru; RP, Río Paraná Delta; WW, White-water Floodplain. Values in parentheses indicate estimated mean annual precipitation (mm/yr).

assigned to the four “classes” of species: 1) “ubiquitous,” present in all OGUs; 2) “widely distributed,” present in 6 OGUs; 3) “intermittent,” present in 4–5 OGUs; and 4) “rarely shared,” restricted to 2–3 OGUs. It should be noted that these labels were not intended to represent actual species distributions; rather, they refer to species distributions within this particular set of OGUs. In all cases, ubiquitous and widely shared species contributed the greatest amount to floristic similarity (52.7–79.2%), with intermittent species accounting for the greatest portion (18.8–39.8%) of the remaining similarity. In all cases, rarely shared species contributed relatively little (1.9–13.4%) to overall floristic similarity.

DISCUSSION

Vegetation description. The Chapare wetlands were distinct from wetlands of other South American lowlands regions, both in floristic composition and structure. Floating vegetation mats, a typical feature of lowland Neotropical wetlands (e.g., Junk 1970, 1983), were conspicuously absent from the majority of the Chapare study sites. Exceptions

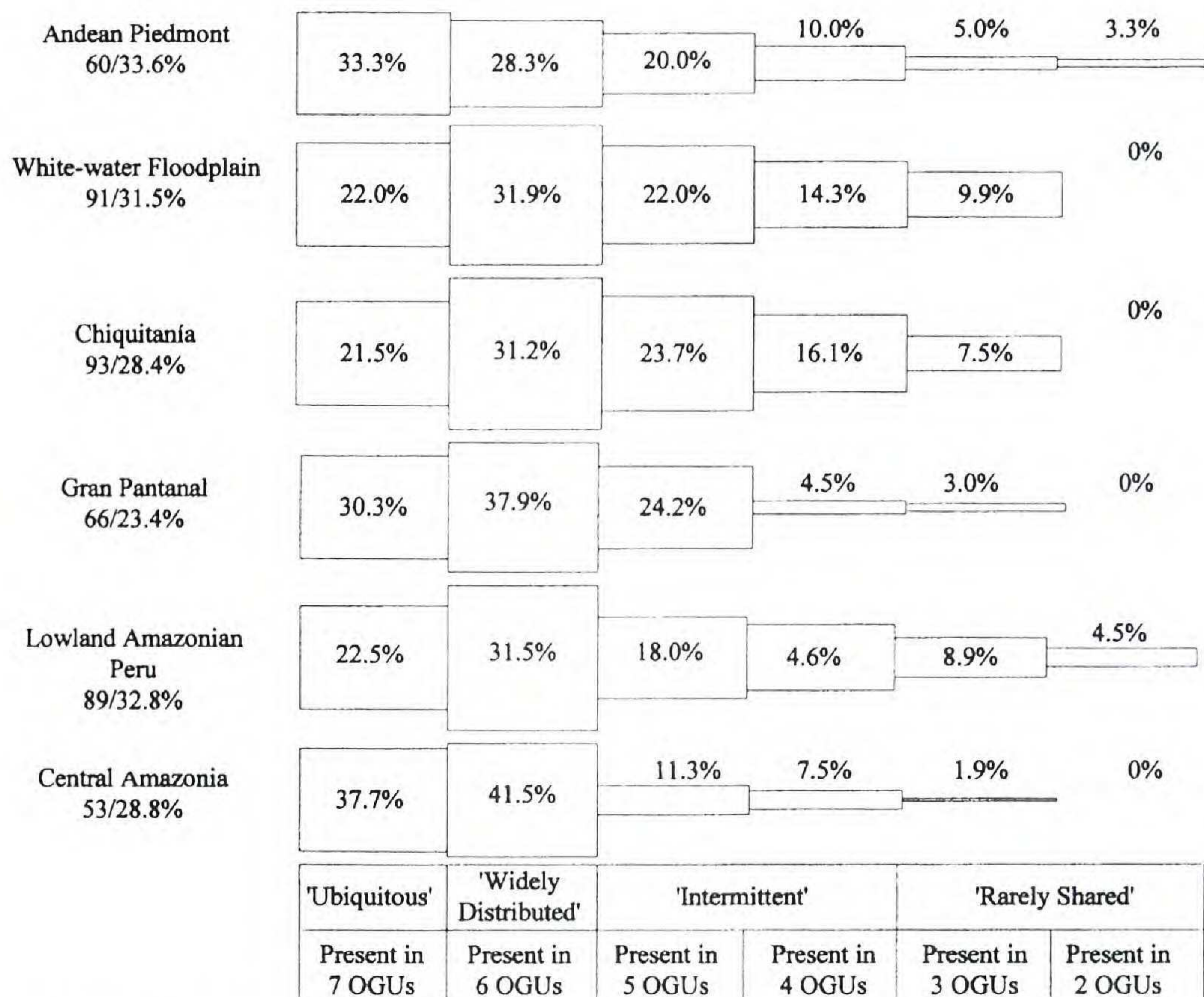


Figure 6. Frequency of species shared between the Chapare and the other Operational Geographic Units (OGUs). Figures below the OGU name indicate the number of species present in both the OGU and the Chapare, followed by floristic similarity (Sørensen's Index). Boxes correspond to species classes (i.e., the number of OGUs in which the species was present) as indicated by the key along the bottom of the figure; the vertical dimension of each box is proportional to the number of species that it represents. Values associated with the boxes indicate the percentage that this portion of the flora contributed to the total species shared between the OGU and the Chapare.

were the Ivirgarsama Marsh, which possessed a well-developed floating mat of *Eleocharis acutangula*, and a few other systems visited during general reconnaissance that possessed poorly developed mats of *Poaceae* spp. and *Polygonum hydropiperoides*.

Palm swamps, a type of wetland that is common throughout the greatest part of the Bolivian lowlands (e.g., Balslev and Moraes 1989; Beck 1984; Moraes 1991), were not encountered in the Chapare. While it may well be that palm swamps were present in the region, none were observed during this study. Likewise, in the distribution of Bolivian palms presented by Balslev and Moraes (1989) no "wetland palms" [e.g., *Copernicia alba* Morong, *Euterpe precatoria* C. Mart., *Mauritia flexuosa* L. f., *Mauritiella armata* (Mart.) Burret] were listed for the Chapare.

The aquatic herb *Eichhornia azurea* Kunth (Pontederiaceae) is ubiquitous throughout most areas of the Bolivian lowlands, where it frequently contributes to the formation of extensive floating mats of vegetation. Nevertheless, *E. azurea* was not noted in the Chapare. A closely related species, *E. crassipes*, is also commonly encountered in the wetlands of lowland Bolivia and occurs in abundance in some wetlands of the dry Interandean Valleys of the Bolivian Andes (Ritter 2000). Yet, *E. crassipes* was rare in the Chapare. This species was not encountered during fieldwork for this study, nor was it listed for the region by Jiménez (1984); however, Maldonado et al. (1996) did cite a single population.

Submerged macrophytes were not well-represented, with only a few species noted: *Myriophyllum mattogrossense* (Haloragaceae), *Mayaca longipes* (Mayacaceae), and *Eichhornia diversifolia* (Pontederiaceae). The genus *Ludwigia* (Onagraceae) was well-represented (7 species, Appendix). Nevertheless, *L. helminthorrhiza* (Mart.) H. Hara and *L. sedioides* (Humb. & Bonpl.) H. Hara, two aquatic species *sensu stricto* that are very common in other Bolivian lowland regions, were not encountered in the Chapare. The Lentibulariaceae were also poorly represented, with the ubiquitous *Utricularia gibba* the sole species encountered. In contrast, this family was well-represented in the Chiquitanía (17 spp. in two genera), Gran Pantanal (10 spp.), and White-water Floodplain (8 spp.) regions (Ritter 2000).

Despite the Chapare's small wetland flora relative to other Bolivian lowland regions (Table 2), a number of noteworthy species were present. The herb *Tonina fluviatilis* (Eriocaulaceae) covered portions of the Mariposa Wetland. Although the Eriocaulaceae are fairly well-represented in Bolivia's wetlands, with at least 5 genera and 17 species (Ritter 2000), *T. fluviatilis* was the sole member of the family encountered in the Chapare. Although *T. fluviatilis* is widely distributed (Mexico to Central South America, Cuba, and Trinidad; Huft 1994), in Bolivia this species is apparently known only from three widely separated sites: the Mariposa Wetland, a wetland in the Pando (extreme northern Bolivia), and a recently encountered population in eastern Bolivia, in Parque Nacional Noel Kempff Mercado (Ritter 2000). Surprisingly, despite the appreciable fieldwork undertaken by Haase and Beck in the extensive inundated savannas of central Bolivia (Beck 1984; Haase 1989, 1990; Haase and Beck 1989), this species apparently is yet to be collected in that region.

The submersed macrophyte *Apalante granatensis* (Hydrocharitaceae) was present in abundance in the Senda F Wetland. Although this species possesses a fairly broad distribution (Colombia to Bolivia), it was previously reported for Bolivia from a single population (Cook 1985).

Nevertheless, *A. granatensis* was observed in a number of roadside pools and marshes in the Chapare, with additional populations noted in the Andean Piedmont region (Ritter 2000).

The wetland shrub *Ludwigia latifolia* (Onagraceae) is also widely distributed, ranging from Nicaragua southwards to Brazil and Bolivia (Ramamoorthy and Zardini 1987). In Bolivia, *L. latifolia* was previously known from a single record: a population in the Chapare along the Río Isarsama. Nevertheless, *L. latifolia* appeared to be fairly common in this region, as during this study additional populations were encountered along three streams.

Other noteworthy species were the rare *Myriophyllum mattogrossense* (Haloragaceae), a submersed macrophyte which had previously not been known for the country (see Crow and Ritter 1999), and the waterlily *Nymphaea glandulifera* (Nymphaeaceae), which was previously known for Bolivia from a single population in the White-water Floodplain (see Ritter et al. 2001). The Chapare appeared to constitute the southern limit for a number of wetland species (e.g., *N. glandulifera*, *Ludwigia latifolia*, *Apalante granatensis*, *M. mattogrossense*, and *Tonina fluviatilis*).

Biodiversity. Based solely on number of species, the Chapare study sites could be characterized as species-poor. These systems each possessed only 5–49 species (Table 1), while systems from the other Bolivian lowland OGUs ranged in richness from 25–124 species (Ritter 2000). Nevertheless, there were large-scale differences in the areas of the sites considered in this comparison (i.e., 0.15 ha in the smallest Chapare site to > 30,000 ha in the largest lowland Bolivian site) and larger sites would generally be expected to contain more species (cf. Rosenzweig 1995).

A more accurate comparison of diversity can be seen in the species-area curve of data from the Chapare sites augmented with data from an additional 16 Bolivian lowland wetland systems (Figure 2). The Chapare sites, with four of seven systems located well below the regression line, could generally be considered as species-poor. However, in a larger study of the wetlands of Bolivia (Ritter 2000), the various wetland types (e.g., ponds, marshes, etc.) were found to be characteristically species-rich or -poor. Three of the four Chapare systems located below the regression line were either ponds or lakes, and these wetland types were generally found to be species-poor (Ritter 2000). Thus, the question arises whether or not the characterization of the wetlands of the Chapare as species-poor was due primarily to the regional sample having a fairly large proportion of species-poor wetland types. Still, as the two least diverse Bolivian

lowland marshes (a species-rich wetland type, Ritter 2000) were from the Chapare, it seems likely that the region's wetlands were, indeed, species-poor.

Additional corroboration of the species-poor nature of Chapare wetlands can be seen in the study of 11 lacustrine systems by Maldonado et al. (1996). While the researchers' primary objectives were the characterization of the physicochemical condition of the lakes and the cataloging of the microflora and microfauna, the authors also compiled a checklist of the systems' vascular plant flora. Their study sites were much larger than the sites considered here (with the exception of the Puerto Villarroel Laguna), ranging in area from 7.75–84.25 ha. In total, 29 species were noted; however, because all specimens were not identified, the authors presented only a partial checklist of 19 species. Site-level species-richness from this portion of the vascular flora ranged from 3–12 species; thus, species-richness could potentially have ranged from 13–22 species (i.e., if all ten unidentified species were present at each site). This level of diversity is even lower than what was encountered at the seven Chapare systems considered here and is much lower than that of equivalent-sized systems in other Bolivian lowland areas. For example, the two study sites listed for the Andean Piedmont region by Ritter (2000) were each about 15 ha in area and possessed 71 and 76 species.

At the regional level, the Chapare possessed the fewest species (113; Table 2), and the Chiquitanía the most species (541). However, as with site-level comparisons, a true measure of diversity requires that regional area also be considered. It would be ideal in a study of wetland habitats if regional area were calculated from just the area of inundated habitats within a region. Although I was able to estimate the extent of inundated area for the Bolivian lowland regions, I was unable to confidently do so for all OGUs considered here. Thus, total regional area was substituted as a surrogate for regional wetland area. As demonstrated in Ritter (2000), this approach appears to be sound. It was evident from a plot of the regional species-area data (Figure 3) that the Chapare could, indeed, be considered species-poor, as it was situated well below the regression line. Other species-poor OGUs were Lowland Amazonian Peru and the White-water Floodplain. By contrast, the Andean Piedmont region, which is contiguous with the Chapare, was the richest OGU.

Low species richness in the Chapare wetlands is not in accordance with what is known for terrestrial habitats in the Andean forelands (e.g., Gentry 1988b; Salo et al. 1986). Gentry (1988a) determined that phytodiversity in the Neotropics was strongly correlated with precipitation. The richest forests were found in high rainfall areas

Table 3. Presence of the Alismatidae and the Alismataceae and estimated mean annual precipitation in selected Operational Geographic Units (OGUs). Precipitation data were estimated from the following sources: the Chapare, Morris et al. (1983); the White-water Floodplain, Andean Piedmont, and Chiquitanía Regions, Hanagarth (1993), Killeen et al. (1993), and the Servicio Nacional de Meteorología e Hidrología, La Paz; Central Amazonia, Ratisbona (1976); Lowland Amazonian Peru, Johnson (1976). Note: the Río Paraná Delta region was excluded from these comparisons because it is situated far outside of the limits of Amazonia.

Region (OGU)	Mean Annual Precipitation (mm/yr)	Alismatidae			
		Families	Overall		Alismataceae
			Genera	Species	Species
Gran Pantanal	1100	5	9	23	13
Chiquitanía	1200	5	8	15	10
White-water Floodplain	1650	5	8	15	9
Andean Piedmont	1700	5	9	12	4
Central Amazonia (Brazil)	2000	3	3	3	1
Lowland Amazonian Peru	2600	5	9	18	11
Chapare	3500	3	4	4	1

(3000–4000 mm) with an aseasonal distribution of precipitation (Gentry 1988a, 1992). Gentry (1988a) also noted that under very wet conditions the relationship became linear, with an asymptote reached at annual precipitation levels of around 4000–4500 mm.

Nevertheless, the low diversity of the Chapare wetlands was not entirely unexpected, as a positive correlation between species richness and a pronounced dry season had previously been noted in one group of aquatic plants by Haynes and Holm-Nielsen (1989). The authors noted a scarcity of species in the subclass Alismatidae in Neotropical regions that did not experience a pronounced wet-and-dry seasonality. Assuming that areas with low mean annual precipitation will generally possess a longer dry season than areas with high mean annual precipitation, this correlation can be evidenced among the OGUs considered here (Table 3). Two of the three wettest OGUs (the Chapare and Central Amazonia) were clearly poorest in representatives of the Alismataceae, and of the Alismatidae in general, while the driest OGUs were generally richest. An exception was the third “wet” OGU, Lowland Amazonian Peru, which possessed the second greatest number of species at both the subclass and familial levels. Nevertheless, Lowland Amazonian Peru does include areas with relatively low annual precipitation (Instituto Geográfico

Nacional 1989); hence, it seems reasonable that at least a portion of the species of Alismatidae noted for this region were restricted to these drier areas.

A similar pattern was evident when considering the total wetland floras of the OGUs. It can be seen from the plot of the regional species-area data (Figure 3) that both the wettest (Chapare) and the third-wettest (Lowland Amazonian Peru) OGUs could be considered as species-poor (i.e., situated below the regression line) OGUs. Additionally, a negative correlation between species richness and precipitation can be evidenced in the difference in diversity between the Chapare and the Andean Piedmont. These regions were approximately equal in area (Table 2) and were situated adjacent to each other along the base of the Andes. Yet, the markedly drier Andean Piedmont region (mean annual precipitation = ca. 1700 mm/yr) possessed more than twice as many wetland species (244 spp.; Table 2) as the Chapare (113 spp.). Furthermore, in the comparison with the general trend of diversity in the Neotropical wetland flora (Figure 3) the Andean Piedmont region was shown to be pronouncedly more diverse. I am inclined to think that if species richness and precipitation data were compiled from a series of small, equal-area samples (i.e., 5000 km²), commencing with the Chapare and proceeding northwards and eastwards out onto the Beni basin, a negative correlation between these two factors would be demonstrated. The current state of both botanical and meteorological data from this region precludes this comparison.

Factors other than precipitation are thought to contribute to the high levels of phytodiversity in Amazonia. The long-held view of Amazonian rainforests has emphasized stability, with forest regeneration seen as occurring predominantly in gaps from treefall (Salo et al. 1986). But, in the last two decades, researchers investigating the effects of floodplain dynamics on lowland Amazonian forests have formulated various hypotheses regarding the contribution of hydrology to forest formation, structure, and diversity (e.g., Kalliola et al. 1991; Puhakka et al. 1992; Salo 1987; Salo et al. 1986). It is now recognized that a significant portion of lowland Amazonian forest is growing upon substrata of fluvial origin. In western Amazonia even forests that are currently unflooded have their origins in the processes that are characteristic along present-day rivers (Kalliola et al. 1991). The lateral erosion and channel migration of the meandering rivers in this region are thought to bring about large-scale natural disturbance and initiate primary succession (Salo et al. 1986). Accretion, erosion, and channel migration serve as a constant form of disturbance in this region, creating a mosaic of forests of different age structure; approximately 0.2% of the area of the active

meander plains and 0.02% of the Peruvian lowlands is eroded annually through these processes (Puhakka et al. 1992).

Salo et al. (1986) proposed that the high levels of disturbance associated with the effects of current and past river dynamics is partially responsible for the elevated biological diversity of the upper Amazon basin. They suggested that: 1) erosion and deposition created a variety of habitats, which, as forest succession and erosion went forward, resulted in a mosaic of different aged forest and soil types; 2) competitive exclusion was precluded because these habitats were fairly short-lived and were highly stable in species composition; and 3) there was a large degree of variation in water and soil chemistry, mode of sedimentation, and “case-historical biogeographical events” (Salo et al. 1986, p. 257). The authors also proposed that, as a result of the high site turnover, intense disturbance, and the resulting varied forest structure, fluvial dynamics might be a major factor in creating and maintaining the high β -diversity characteristic of the upper Amazon basin. Nevertheless, as Puhakka et al. (1992) have pointed out, the relationship between vegetation patterns and river types are poorly understood; hence, it is difficult to assess the influence that fluvial dynamics may have had on a region’s biota.

Although fluvial dynamics may be positively linked with phytodiversity in lowland Amazonian terrestrial habitats, these forces appear to negatively impact the Chapare’s wetlands. As river channels shift, oxbow and strand lakes are frequently formed. Many of these persist as lacustrine systems, but others may be reincorporated into the river’s mainstem when the sediment dams separating them from the main channel are breached by flooding and erosion. These transitions can occur over a fairly short period of time. For example, during field research a journey was taken up the Río Ichilo to visit a large (ca. 8 km long) oxbow lake that had formed approximately two years previously (based on estimates provided by local fishermen). Upon arrival, it was found that the barriers separating the oxbow from the river had eroded, and the oxbow was once again joined with the Ichilo.

Nevertheless, many of these systems can persist as isolated basins and will undergo various stages of lake-fill (i.e., “successional stages”) over time. I examined a number of such systems during this study and all appeared to be species-poor. The flora differed from system to system but, in contrast to what is known for Amazonian terrestrial habitats, it was not evident that there were particular sets of species associated with various successional stages. Furthermore, in Bolivian lowland wetlands it appeared that systems with well-developed floating mats of vegetation generally were the most speciose, in part because of the capability of

these mats to become secondarily colonized by other taxa. As noted, floating mats were generally lacking or poorly developed in Chapare wetlands, and it seems likely that the aforementioned fluvial dynamics have contributed to their scarcity.

In extensive areas of lowland South America, wetlands are subjected to large-scale, regular, seasonal hydrological pulses. Rather than functioning as a disturbance and therefore limiting species richness, some researchers consider that these regular, monomodal pulses enhance diversity (e.g., Junk 1997; Junk et al. 1989; Prado et al. 1994). The rivers of the Chapare, however, do not experience regular seasonal pulses. Instead, they fluctuate in response to precipitation in the upslope regions from which their tributaries flow. Although it may be that the absence of a monomodal hydrologic pulse is associated with the low diversity of the Chapare wetlands, there is still some question as to whether or not these pulses characteristically have a positive effect on phytodiversity (see Ritter 2000).

Any discussion of Chapare ecosystems needs to take into account anthropogenic disturbance. As noted, extensive portions of the Chapare have been converted to the production of coca (*Erythroxylum coca*), with the greatest part intended for the manufacture of cocaine. Enormous quantities of various chemicals (e.g., ammonia, ether, kerosene, potassium permanganate, sodium bicarbonate, and sulfuric acid; Henkel 1995) are used each year in the extraction of coca paste, the first step of cocaine processing. As of the early 1990s, an estimated 4000–5000 coca paste-producing laboratories were operating in the Chapare, with the chemicals used in the extraction process disposed of on site. Although it seems likely that diversity in the Chapare might be negatively impacted by such extensive chemical pollution, there is some evidence that this is not yet the case (Southwest Research Associates Inc. 1993, cited in Henkel 1995). Nevertheless, the region has unquestionably been subjected to extensive anthropogenic modifications in recent decades, and the assumption that these activities must have had some negative impact on diversity in the region's wetlands seems warranted.

Floristic similarities. At the site level, floristic similarities (Sørensen's Index) were generally low, ranging from 0–43%. In contrast, floristic similarities between aquatic systems of the Bolivian portion of the Gran Pantanal de Mato Grosso ranged from 39–58% (Ritter 2000). All of the systems in the Pantanal study (with one exception) were much larger (i.e., 3000–20,000 ha) than the Chapare sites, all but one of which were less than 2 ha. Thus, the Chapare site's low floristic similarities were

undoubtedly partially attributable to sample size. Furthermore, despite their generally low floristic similarities, the majority of the Chapare study sites were situated in close proximity in an ordination (DCA) of the 46 Bolivian study sites (Figure 4). The two systems that were disjunct (in ordination space) from the other Chapare study sites had extremely small floras (5 and 6 species), and their positions in the ordination were most likely due to their possessing one or two species that were common in most lowland systems but absent from the other Chapare sites.

As all but one of the Chapare sites were quite small, it is not clear whether the low floristic similarities were the result of high β -diversity in the region's wetland flora, or if they were merely an artifact of system size. To elaborate, regions will possess a number of common species (which will serve to elevate calculated floristic similarities), and as the number of species present in small sites will, on average, be less than in large sites, the number of common (and thus, commonly shared) species encountered in small sites will, on average, be less than in large sites.

At the regional scale, the Chapare wetland flora appeared to possess equivalent floristic affinities (as calculated by Sørensen's Index) with the more northern Amazonian OGUs as with the other Bolivian lowland regions. However, the ordination of OGU floras by DCA (Figure 5) indicated that, as might be expected, the Chapare was more closely associated with the lowland Bolivian OGUs than with the extra-Bolivian Amazonian OGUs.

Although the ordination suggested a close floristic association among the lowland Bolivian OGUs, this relationship was not nearly so evident from the histograms of the species frequency classes (Figure 6). The relationships between the Chapare wetland flora and the other OGUs consistently followed the same general pattern, with "ubiquitous" (present in all OGUs) and "widely shared" species (present in six OGUs) contributing the greatest amount to floristic similarities. The largest contribution of "rarely shared" species (restricted to 2–3 OGUs) to floristic similarity was between the Chapare and the spatially disjunct (both geographically and in ordination space; Figure 5) Lowland Amazonian Peru (13.4%). It had been hoped that both the ordination and the frequency analysis would provide evidence that the "wetter" OGUs were closely associated; however, in neither case was a close relationship suggested.

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APPENDIX

SPECIES ASSOCIATED WITH WETLANDS IN THE CHAPARE REGION

Taxa marked with an asterisk (*) are considered to be non-native to Bolivia, as determined from the literature. Abbreviations for study sites are as follows: MW, Mariposa Wetland; IM, Ivirgarsama Marsh; SF, Senda F Wetland; VT, Villa Tunari Pond; SP, Sinahota Pond; PV, Puerto Villarroel Laguna; SC, Valle de Sajta Curichi; GC, General Collecting. Abbreviations for abundance are as follows: A, Abundant; F, Frequent; C, Common; O, Occasional; R, Rare; LA, Locally Abundant; NN, Not Noted. Taxa without listed voucher specimens are those known to be associated with Neotropical wetlands or that were noted in the Chapare by other researchers [data compiled from Jiménez 1984, Maldonado et al. 1993, and w³TROPICOS (Missouri Botanical Garden VAST nomenclatural database. Website: <http://mobot.mobot.org/3WT/Search/vast.html>)].

POLYPODIOPHYTA (Ferns)

- HYMENOPHYLLACEAE.** *Trichomanes rigidum* Sw. – Emergent herb; GC/NN.
- LYCOPODIACEAE.** *Lycopodium clavatum* L. – Trailing herb; MW/O, IM/LA *N. Ritter 3821* (BOLV, LPB, MO, NHA).
- MARATTIACEAE.** *Danaea elliptica* Sm. – Emergent herb; GC/NN.
- PTERIDACEAE.** *Ceratopteris pteridoides* (Hook.) Hieron. – Free-floating herb; SC/F, GC/A *N. Ritter 1685* (BOLV, LPB, MO, NHA, W). *Pityrogramma calomelanos* (L.) Link – Emergent herb; IM/O *N. Ritter 3161* (BOLV, NHA).
- SALVINIACEAE.** *Salvinia minima* Baker – Free-floating herb; SC/F *N. Ritter 1689* (BOLV, LPB, MO, NHA).
- THELYPTERIDACEAE.** *Thelypteris interrupta* (Willd.) K. Iwats. – Emergent herb; IM/C *N. Ritter 2980* (BOLV, LPB, MO, NHA, W). *Thelypteris serrata* (Cav.) Alston – Emergent herb; MW/C, IM/C, VT/R *N. Ritter 3156* (BOLV, NHA). *Thelypteris* sp. – Emergent herb; IM/LA *N. Ritter 3820* (BOLV, LPB, MO, NHA, W).

MAGNOLIOPHYTA (Angiosperms)

MAGNOLIOPSIDA (Dicotyledons)

ACANTHACEAE. *Hygrophila costata* Nees – Emergent herb; GC/LA *N. Ritter 3148* (BOLV, LPB, MO, NHA, USZ). *Justicia comata* (L.) Sw. – Emergent herb; VT/A, GC/LA *N. Ritter 1613* (BOLV, LPB, MO, NHA, W).

ANACARDIACEAE. *Tapirira guianensis* Aubl. – Tree; GC/NN.

APOCYNACEAE. *Mandevilla hirsuta* (Rich.) K. Schum. – Climber; MW/O *N. Ritter 3849* (BOLV, LPB, MO, NHA). *Odontadenia geminata* (Hoffmanns. ex Roem. & Schult.) Müll.Arg. – Climber; MW/R *N. Ritter & M. Ritter 3853* (BOLV, NHA). *Prestonia acutifolia* (Benth. ex Müll.Arg.) K. Schum. – Climber; SF/O *N. Ritter 1620* (BOLV, LPB, MO, NHA). *Rhabdadenia macrostoma* (Benth.) Müll.Arg. – Climber; SC/O *N. Ritter 1688* (BOLV, LPB, MO, NHA).

ASCLEPIADACEAE. *Cynanchum montevidense* Spreng. – Climber; GC/O *N. Ritter & M. Ritter 3855* (BOLV, MO, NHA). *Tassadia grazielae* Fontella – Climber; MW/A, IM/LA *N. Ritter 1439* (BOLV, LPB, MO, NHA, W).

ASTERACEAE. *Barrosoa confluentis* (B. L. Rob.) R. M. King & H. Rob. – Emergent herb; IM/R *N. Ritter 2985* (BOLV, LPB, MO, NHA, W). *Eclipta prostrata* (L.) L. – Emergent herb; SP/R *N. Ritter 1439* (BOLV, MO, NHA). **Erechtites hieraciifolia* Raf. ex DC. – Emergent herb; IM/O *N. Ritter 3833* (BOLV, NHA). *Mikania congesta* DC. – Climber; SF/C *N. Ritter 3141* (BOLV, MO, NHA). *Mikania psilostachya* DC. – Climber; MW/F *N. Ritter 1641* (BOLV, LPB, MO, NHA, W). *Tessaria integrifolia* Ruiz & Pav. – Tree; GC/A.

BEGONIACEAE. *Begonia fischeri* Schrank – Emergent herb; IM/O *N. Ritter 2981* (BOLV, NHA, USZ).

BORAGINACEAE. *Cordia tetrandra* Aubl. – Tree; GC/NN.

CABOMBACEAE. *Cabomba furcata* Schult. & Schult. f. – Submersed herb; GC/A *N. Ritter 3812* (BOLV, LPB, MO, NHA).

CAMPANULACEAE. *Centropogon cornutus* (L.) Druce – Emergent herb; MW/LA, IM/C *N. Ritter & G.E. Crow 2310* (BOLV, LPB, MO, NHA, W).

CHRYSOBALANACEAE. *Hirtella triandra* Sw. – Tree; GC/NN.

CLUSIACEAE. *Calophyllum brasiliense* Cambess. – Tree; GC/NN. *Vismia* sp. – Tree; IM/R *N. Ritter 3818* (BOLV, NHA).

CONVOLVULACEAE. *Ipomoea* cf. *phillomega* House – Climber; IM/O *N. Ritter 3163* (BOLV, LPB, NHA).

DILLENIACEAE. *Davilla nitida* (Vahl) Kubitzki – Climber; IM/R *N. Ritter 3816* (BOLV, MO, NHA).

ERYTHROXYLACEAE. *Erythroxylum coca* Lam. – Shrub; IM/R N. Ritter 3819 (BOLV, MO, NHA).

EUPHORBIACEAE. *Capersonia palustris* (L.) A. St.-Hil. – Emergent herb, at times free-floating; SF/O, GC/C N. Ritter 1399 (BOLV, LPB, MO, NHA, W).

FABACEAE. *Aeschynomene rudis* Benth. – Emergent herb; GC/A N. Ritter & G.E. Crow 2315 (BOLV, LPB, MO, NHA, W). *Desmodium adscendens* (Sw.) DC. – Climber; MW/C, IM/C N. Ritter 3825 (BOLV, NHA). *Inga umbellifera* (Vahl) Steud. ex DC. – Tree; GC/NN. *Mimosa pigra* L. – Shrub; GC/F N. Ritter 1399 (BOLV, LPB, MO, NHA). *Phaseolus* sp. – Climber; MW/R, IM/C N. Ritter 3825 (BOLV, NHA). *Zygia cauliflora* (Willd.) Killip ex Record – Tree; SF/O N. Ritter & G.E. Crow 1121 (BOLV, MO, NHA). Indet. – Emergent herb; MW/C N. Ritter 3846 (BOLV, NHA).

HALORAGACEAE. *Myriophyllum mattogrossense* Hoehne – Submersed herb; GC/LA N. Ritter 3147 (BOLV, GH, LPB, MO, NHA, USZ).

LAMIACEAE. *Hyptis atrorubens* Poit. – Emergent herb; MW/LA N. Ritter 1636 (BOLV, LPB, MO, NHA, W). *Hyptis brevipes* Benth. – Emergent herb; SP/O N. Ritter 1395 (BOLV, LPB, MO, NHA). *Hyptis lacustris* A. St.-Hil. ex Benth. – Emergent herb; IM/O N. Ritter 3157 (BOLV, LPB, MO, NHA).

LENTIBULARIACEAE. *Utricularia gibba* L. – Suspended aquatic herb; IM/O N. Ritter 3836 (BOLV, NHA).

LORANTHACEAE. *Phthirusa pyrifolia* (Kunth) Eichler – Parasite; MW/C, IM/O N. Ritter 3847 (BOLV, LPB, MO, NHA).

LYTHRACEAE. *Cuphea melvilla* Lindl. – Shrub; PV/F N. Ritter 1680 (BOLV, LPB, MO, NHA, W).

MALVACEAE. *Hibiscus sororius* L. – Emergent herb; PV/O N. Ritter 1682 (BOLV, LPB, MO, NHA, W). *Pavonia fruticosa* (P. Mill.) Fawc. & Rendle – Emergent herb; VT/O N. Ritter 1646 (BOLV, LPB, MO, NHA, W).

MELASTOMATACEAE. *Aciotis acuminifolia* (Mart. ex DC.) Triana – Emergent herb; MW/O, IM/LA, GC/LA N. Ritter 1637 (BOLV, LPB, MO, NHA, W). *Aciotis caulialata* (Ruiz & Pav.) Triana – Emergent herb; MW/O N. Ritter 3842 (BOLV, MO, NHA). *Clidemia* cf. *biserrata* DC. – Shrub; MW/C N. Ritter 1640 (BOLV, LPB, MO, NHA, W). *Clidemia capitellata* (Bonpl.) D. Don – Shrub; IM/NN N. Ritter 3158 (BOLV, MO, NHA, US). *Miconia ampla* Triana – Shrub; MW/A, IM/R N. Ritter & G.E. Crow 2294 (BOLV, LPB, MO, NHA, W). *Miconia tomentosa* (Rich.) D. Don – Shrub; IM/R N. Ritter 3815 (BOLV, LPB, MO, NHA, US). *Miconia* sp. – Shrub; MW/O N. Ritter 3840 (BOLV, LPB, MO, NHA, US). *Tococa* aff. *macrophysca* Spruce ex Triana – Shrub; MW/LA N. Ritter & G.E. Crow 2295 (BOLV, GH, LPB, MO, NHA, US, W).

MYRTACEAE. *Eugenia florida* DC. – Understory tree; GC/NN. **Psidium guajava* L. – Understory tree; VT/O N. Ritter 1400 (BOLV, LPB, MO, NHA, W).

NYMPHAEACEAE. *Nymphaea amazonum* Mart. & Zucc. subsp. *amazonum* – Rooted macrophyte with floating leaves; GC/C N. Ritter & G.E. Crow 2316 (BOLV, LPB, MO, NHA, W). *Nymphaea glandulifera* Rodsch. – Rooted macrophyte with floating leaves; MW/LA N. Ritter 1642 (BOLV, MO, NHA).

OCHNACEAE. *Sauvagesia erecta* L. – Emergent herb; MW/C, IM/C N. Ritter 1633 (BOLV, LPB, MO, NHA, W).

ONAGRACEAE. *Ludwigia affinis* (DC.) Hara – Emergent herb; GC/R N. Ritter 3137 (BOLV, NHA). *Ludwigia decurrens* Walter – Emergent herb; IM/O, GC/LA N. Ritter & G.E. Crow 3839 (BOLV, GH, LPB, MO, NHA, W). *Ludwigia inclinata* (L. f.) M. Gómez – Emergent herb; SF/C, GC/A N. Ritter 1614 (BOLV, LPB, MO, NHA, W). *Ludwigia latifolia* (Benth.) Hara – Shrub; GC/O N. Ritter 2987 (BOLV, LPB, MO, NHA, W). *Ludwigia leptocarpa* (Nutt.) Hara – Emergent herb; SC/O, PV/O, GC/C N. Ritter 2977 (BOLV, LPB, MO, NHA, W). *Ludwigia nervosa* (Poir.) Hara – Shrub; MW/A, IM/A, SF/C N. Ritter & G.E. Crow 1112 (BOLV, LPB, MO, NHA). *Ludwigia octovalvis* (Jacq.) Raven – Emergent herb; SF/C, SP/C N. Ritter 1392 (BOLV, LPB, MO, NHA, W).

PIPERACEAE. *Piper pilirameum* C. DC. – Shrub; MW/C, IM/O N. Ritter 1639 (BOLV, LPB, MO, NHA, W).

POLYGONACEAE. *Polygonum ferrugineum* Wedd. – Emergent herb; GC/LA N. Ritter & G.E. Crow 1133 (BOLV, LPB, MO, NHA). *Polygonum hydropiperoides* Michx. – Emergent herb; MW/C, IM/O, SP/F, GC/A N. Ritter 1391 (BOLV, LPB, MO, NHA, W). *Polygonum meisnerianum* Cham. & Schldl. – Emergent herb; GC/LA N. Ritter 1615 (BOLV, LPB, MO, NHA, W). *Polygonum punctatum* Elliott – Emergent herb; SC/A, PV/F N. Ritter 1687 (BOLV, LPB, MO, NHA, W). *Triplaris americana* L. – Tree; GC/NN.

RUBIACEAE. *Borreria ocymifolia* (Willd. ex Roem. & Schult.) Bacigalupo & E. L. Cabral – Emergent herb; GC/LA N. Ritter 1702 (BOLV, LPB, MO, NHA, W). *Coccocypselum hirsutum* Bartl. ex DC. – Emergent herb; MW/LA N. Ritter & G.E. Crow 2300 (BOLV, LPB, MO, NHA). *Genipa americana* L. – Tree; GC/NN. **Oldenlandia lancifolia* (Schumach.) DC. – Emergent herb; MW/O, IM/O, SF/C, VT/C, SP/F, GC/F N. Ritter 1701 (BOLV, LPB, MO, NHA, W). *Palicourea riparia* Benth. – Shrub; SF/O N. Ritter & G.E. Crow 1118 (BOLV, MO, NHA). *Palicourea triphylla* DC. – Shrub; IM/R N. Ritter 3823 (BOLV, LPB, MO, NHA, USZ, W). *Psychotria poeppigiana* Müll.Arg. – Shrub; MW/F N. Ritter & G.E. Crow 2309 (BOLV, GH, MO, NHA, W). *Sabicea novo-granatensis* K. Schum. – Climber; MW/A, IM/O, SF/C, GC/O N. Ritter 1438 (BOLV, LPB, MO, NHA, W). *Sabicea villosa* Willd. ex Roem. & Schult. – Climber; GC/NN. *Spermacoce tenuior* L. – Emergent herb; VT/LA N. Ritter 1407 (BOLV, LPB, MO, NHA, W).

SAPINDACEAE. *Paullinia pinnata* L. – Climber; SF/O N. Ritter & G.E. Crow 1120 (BOLV, LPB, NHA).

SCROPHULARIACEAE. *Lindernia* sp. – Emergent herb; SP/LA N. Ritter 1387 (BOLV, LPB, MO, NHA, W). *Scoparia dulcis* L. – Emergent herb; GC/NN. **Torenia thouarsii* (Cham. & Schldl.) O. Kuntze – Emergent herb; MW/O, IM/R, GC/C N. Ritter 1700 (BOLV, LPB, MO, NHA).

SPHENOCLEACEAE. *Sphenoclea zeylanica* Gaertn. – Emergent herb; GC/R.

VITACEAE. *Cissus erosa* Rich. – Climber; GC/LA *N. Ritter 1694* (BOLV, LPB, MO, NHA, W).

LILIOPSIDA (Monocotyledons)

ALISMATACEAE. *Echinodorus* cf. *subalatus* (Mart.) Griseb. – Emergent herb; SF/O *N. Ritter 1617* (BOLV, LPB, MO, NHA, UNA).

ARACEAE. *Pistia stratiotes* L. – Free-floating herb; GC/NN.

COMMELINACEAE. *Commelina* sp. – Emergent herb; MW/NN *N. Ritter 1442* (BOLV, MO, NHA).

COSTACEAE. *Costus arabicus* L. – Emergent herb; IM/F *N. Ritter 3152* (BOLV, MO, NHA). *Costus scaber* Ruiz & Pav. – Emergent herb; GC/NN.

CYPERACEAE. *Calyptracarya glomerulata* (Brongn.) Urb. – Emergent herb; MW/LA *N. Ritter & G.E. Crow 2305* (BOLV, MO, NHA, W). *Cyperus aggregatus* (Willd.) Endl. – Emergent herb; GC/LA *N. Ritter 3810* (BOLV, LPB, MO, NHA, W). *Cyperus haspan* L. – Emergent herb; MW/F, IM/R *N. Ritter 1635* (BOLV, MO, NHA, W). *Cyperus luzulae* Hochst. ex Steud. – Emergent herb; IM/O, SF/C, VT/C *N. Ritter 3834* (BOLV, MO, NHA). *Cyperus meyenianus* Kunth – Emergent herb; MW/R, IM/C, SF/O *N. Ritter 3814* (BOLV, LPB, MO, NHA, W). *Cyperus surinamensis* Rottb. – Emergent herb; SP/F *N. Ritter 1394* (BOLV, MO, NHA). *Diplacrum longifolium* (Griseb.) C. B. Clarke – Emergent herb; MW/F *N. Ritter 1630* (BOLV, MO, NHA, W). *Diplasia karataefolia* Rich. – Emergent herb; MW/R *N. Ritter & G.E. Crow 2307* (BOLV, MO, NHA, W). *Eleocharis acutangula* (Roxb.) Schult. – Floating mat-forming herb; IM/A *N. Ritter 2979* (BOLV, LPB, MO, NHA, W). *Eleocharis elegans* (Kunth) Roem. & Schult. – Emergent herb; GC/O *N. Ritter 3135* (BOLV, MO, NHA). *Eleocharis interstincta* R. Br. – Emergent herb; MW/A *N. Ritter 1433* (BOLV, MO, NHA). *Fimbristylis dichotoma* (L.) Vahl – Emergent herb; IM/LA, GC/C *N. Ritter 1704* (BOLV, MO, NHA, W). *Fimbristylis littoralis* Gaudich. – Emergent herb; GC/F *N. Ritter 2978* (BOLV, LPB, MO, NHA, W). *Oxycaryum cubense* (Poepp. & Kunth) Lye – Floating mat-forming herb; IM/O *N. Ritter 3165* (BOLV, NHA). *Scleria cyperinoides* Clark – Emergent herb; MW/C *N. Ritter & G.E. Crow 2299* (BOLV, MO, NHA). *Scleria macrophylla* J. Presl & C. Presl – Emergent herb; MW/LA, SF/C, GC/C *N. Ritter 3150* (BOLV, LPB, MO, NHA). *Scleria microcarpa* Nees ex Kunth – Emergent herb; SF/O, VT/A *N. Ritter 1402* (BOLV, MO, NHA, W).

ERIOCAULACEAE. *Tonina fluviatilis* Aubl. – Emergent herb; MW/A *N. Ritter 1443* (BOLV, LPB, MO, NHA).

HELICONIACEAE. *Heliconia marginata* (Griggs) Pittier – Emergent herb; SC/A *N. Ritter 1686* (BOLV, LPB, MO, NHA).

HYDROCHARITACEAE. *Apalanthe granatensis* (Humb. & Bonpl.) Planch. – Submersed herb; SF/A *N. Ritter 1621* (BOLV, LPB, MO, NHA, W). *Limnobium laevigatum* (Humb. & Bonpl. ex Willd.) Heine – Free-floating herb; GC/NN.

LIMNOCHARITACEAE. *Limnocharis flava* (L.) Buchenau – Emergent herb; GC/R N. Ritter 1616 (BOLV, LPB, MO, NHA, W).

ORCHIDACEAE. *Campylocentrum minutum* C. Schweinf. – Epiphytic herb; IM/O N. Ritter 3838 (LPB, MO, NHA, USZ). *Epidendrum schomburgkii* Lindl. – Epiphytic herb; MW/R N. Ritter & G.E. Crow (BOLV, MO, NHA). *Trizeuxis falcata* Lindl. – Epiphytic herb; IM/C N. Ritter 3837 (BOLV, LPB, MO, NHA, USZ, W).

POACEAE. *Acroceras zizanioides* (Humb., Bonpl. & Kunth) Dandy – Emergent herb; GC/A N. Ritter 2975 (BOLV, NHA, W). *Andropogon bicornis* (L.) Forsk. – Emergent herb; MW/O, IM/O N. Ritter 3875 (BOLV, NHA). *Andropogon selloanus* (Hack.) Hack. – Emergent herb; MW/O N. Ritter 1634 (BOLV, LPB, MO, NHA). *Axonopus fissifolius* (Raddi) Kuhlm. – Emergent herb; SP/R N. Ritter 1393 (BOLV, LPB, MO, NHA). **Coix lacryma-jobi* L. – Emergent herb; GC/LA. *Echinochloa colona* (L.) Link – Emergent herb; GC/O N. Ritter 2993 (BOLV, LPB, MO, NHA, W). *Gynerium sagittatum* (Aubl.) P. Beauv. – Emergent herb; GC/A. **Hemarthria altissima* (Poir.) Stapf & C. E. Hubb – Emergent herb; GC/LA N. Ritter, J. Wood, D. Brummitt & D. Wasshausen 3265 (BOLV, LPB, MO, NHA). *Homolepis aturensis* (Humb., Bonpl. & Kunth) Chase – Emergent herb; MW/C N. Ritter 1629 (BOLV, LPB, MO, NHA). *Hymenachne amplexicaulis* (Rudge) Nees – Emergent herb; GC/A N. Ritter 1691 (BOLV, LPB, MO, NHA). *Hymenachne donacifolia* (Raddi) Chase – Emergent herb; SF/F N. Ritter 3139 (BOLV, NHA). **Hyparrhenia rufa* (Nees) Stapf. – Emergent herb; IM/F N. Ritter 31 (BOLV, LPB, MO, NHA). *Luziola bahiensis* (Steud.) Hitchc. – Emergent herb; MW/O N. Ritter 1631 (BOLV, LPB, MO, NHA). *Panicum dichotomiflorum* Michx. – Emergent herb; SP/F N. Ritter 1396 (BOLV, LPB, MO, NHA). *Panicum grande* Hitchc. & Chase – Emergent herb; MW/C N. Ritter & G.E. Crow 2308 (BOLV, MO, NHA). *Panicum hylaeicum* Mez – Emergent herb; MW/LA N. Ritter 3843 (BOLV, MO, NHA, US). *Panicum laxum* Sw. – Emergent herb; VT/C N. Ritter 1403 (BOLV, LPB, MO, NHA). *Panicum mertensii* Roth – Emergent herb; PV/C N. Ritter 1679 (BOLV, LPB, MO, NHA). *Panicum pilosum* Sw. – Emergent herb; MW/O, VT/C, GC/LA N. Ritter 2986 (BOLV, LPB, MO, NHA, W). *Panicum polygonatum* Schrad. – Emergent herb; MW/A, IM/LA N. Ritter 3830 (BOLV, LPB, MO, NHA, W). *Panicum schwackeanum* Mez – Emergent herb; MW/F N. Ritter 1434 (BOLV, LPB, MO, NHA). *Panicum stoloniferum* Poir. – Emergent herb; VT/C N. Ritter 1406 (BOLV, LPB, MO, NHA). *Paspalum conjugatum* P. J. Bergius – Emergent herb; GC/NN. *Paspalum repens* P. J. Bergius – Emergent herb; GC/NN. *Steinchisma hians* (Elliott) Nash ex Small – Emergent herb; MW/C N. Ritter 3142 (BOLV, NHA).

PONTEDERIACEAE. *Eichhornia crassipes* (Mart.) Solms – Herb with floating stems and/or petioles (at times free-floating); GC/NN. *Eichhornia diversifolia* (Vahl) Urb. – Herb with floating stems and/or petioles; GC/R N. Ritter 2974 (BOLV, GH, NHA). *Pontederia rotundifolia* L. f. – Herb with floating stems and/or petioles; SF/A N. Ritter 1622 (BOLV, LPB, MO, NHA).